



## A new species of the genus *Norops* from Darién, Panama, with comments on *N. sulcifrons* (Cope 1899) (Reptilia, Squamata, Dactyloidae)

KIRSTEN E. NICHOLSON<sup>1,3</sup> & GUNTHER KÖHLER<sup>2</sup>

<sup>1</sup>Dept. of Biology and Museum of Cultural and Natural History, Central Michigan University, Mt. Pleasant, MI 48859, U.S.A.

<sup>2</sup>Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325 Frankfurt a.M., Germany

<sup>3</sup>Corresponding author. E-mail: [norops@gmail.com](mailto:norops@gmail.com)

### Abstract

We describe the new species *Norops triumphalis* sp. nov. from Darién, Panama. *Norops triumphalis* differs from all congeners by having a combination of (1) smooth, bulging, subimbricate ventral scales; (2) a short tail, ratio tail length/SVL 1.54; (3) short hind legs, longest toe of adpressed hind leg reaching to ear opening, ratio shank length/SVL 0.24; (4) a lichenous body pattern; and (5) a very large yellowish orange dewlap in males. In external morphology, *N. triumphalis* is most similar to the species of the *N. pentaprion* group. *Norops triumphalis* differs from the other species in the *N. pentaprion* group, except *N. sulcifrons*, by having a very large orange male dewlap (vs. a large red or pink dewlap) and an unpigmented throat lining. *Norops triumphalis* differs from *N. sulcifrons* by having the supracaudal scales not forming a serrated crest (vs. a distinct serrated caudal crest present in *N. sulcifrons*), 4 supracaudal scales per segment (vs. 3 supracaudal scales per segment in *N. sulcifrons*), greatly enlarged outer postmental scales, about four times the size of adjacent medial scales (vs. moderately enlarged outer postmental scales, about twice the size of adjacent medial scales, in *N. sulcifrons*), and no enlarged postcloacal scales in males (vs. a pair of moderately enlarged postcloacal scales present in male *N. sulcifrons*). We further provide a standardized description and illustrations of the holotype of *N. sulcifrons*.

**Key words:** Dactyloidae, hemipenial morphology, new species, *Norops triumphalis* sp. nov., Panama, Reptilia, Squamata

### Introduction

The anole species related to *Norops pentaprion* (Cope 1862) form a tight cluster of small to moderate-sized anoles that would fit the criteria of a twig anole sensu Williams (1983). Currently, the following eight Central American species are assigned to the *Norops pentaprion* group sensu Köhler (2010): *N. beckeri* (Boulenger 1881), *N. charlesmyersi* (Köhler 2010), *N. cristifer* (Smith 1968), *N. fungosus* (Myers 1971), *N. pentaprion* (Cope 1862), *N. salvini* (Boulenger 1885), and *N. utilensis* Köhler 1996. Additionally, three South American species have been assigned to this species group: *N. ibague* (Williams 1975), *N. ortonii* (Cope 1868), and *N. sulcifrons* (Cope 1899) (see Myers 1971, Williams 1975). A recent expedition to eastern Panama led by KEN resulted in the collection of a single adult male of an anole that could not be assigned to any of the known species from Central or South America. Based on its external morphology, it is clearly a member of the *N. pentaprion* species group. A thorough comparison with all known species currently assigned to this group confirmed that it represents an undescribed species. Thus, we provide a formal description of this new species below.

### Material and methods

In evaluating whether multiple species exist within a certain species complex, we follow the Evolutionary Species Concept (Simpson 1961; Wiley 1978), and operationalize this concept by identifying species based on consistent differences between populations (Frost & Kluge 1994). Recently, Nicholson *et al.* (2012) proposed a new classification for the anoles. Despite published criticism (Castañeda & de Queiroz 2013; Poe 2013), rebutted by

Nicholson *et al.* (2014), we follow the Nicholson *et al.* (2012) arrangement herein, and thus recognize *Norops* for the beta anoles occurring in Central America. Abbreviations for museum collections follow Sabaj Pérez (2014) except ECOCHH (Museo de Zoología-Ecosur, Chetumal, Quintana Roo, Mexico), MZ-UNICACH (Museo Zoológico de la Universidad de Ciencias y Artes del Estado de Chiapas, Tuxtla Gutiérrez, Chiapas, Mexico), and IHNHERP (Colección Herpetológica del Instituto de Historia Natural, Tuxtla Gutiérrez, Chiapas, Mexico). POE field numbers refer to specimens that will be deposited in the Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A.. Coordinates and elevation were recorded using Garmin GPS receivers with built-in altimeters. All coordinates are in decimal degrees, WGS 1984 datum. The capitalized colors and color codes (the latter in parentheses) are those of Köhler (2012). Terminology of markings used in color descriptions follow Köhler (2012). Nomenclature of scale characters follows that of Köhler (2014). Head length was measured from the tip of the snout to the anterior margin of the ear opening, with the calipers held in a vertical position relative to the head. Snout length was measured from the tip of the snout to the anterior border of the orbit, with the calipers held in a horizontal position relative to the head. Head width was determined with the broad tips of the calipers aligned with the levels of posterior margin of eye and supralabial scales, respectively, with the calipers held in a vertical position relative to the head. Dorsal and ventral scales were counted at midbody along the midline. Tail height and width were measured at the point reached by the heel of the extended hind leg. Subdigital lamellae were counted on Phalanges II to IV of Toe IV of the hind limbs, and separately on distal phalanx. We considered the scale directly anterior to the circumnasal to be a prenasal. Dewlap area was measured following the methods of Köhler (2014). We took photographs of males in life with their dewlaps artificially extended using small forceps. The head portion was magnified and printed and then superimposed on millimetric paper; the total number of millimeter squares contained in the extended dewlap was counted. A straight line was drawn between the anterior and posterior insertions of the dewlap. The HL on the printout was also determined. We used the following equation to convert the magnified dewlap area to the real size:  $X = [(\sqrt{Y/A})B]^2$ , where X is the real area of the dewlap in square millimeters, Y is the total area (square millimeters) of the dewlap at a magnified scale, A is the HL measure (millimeters) of the anole at a magnified scale, and B is the HL measure (millimeters) of the anole at the real size.

## Results

### *Norops triumphalis* sp. nov.

Figs. 1–5

**Holotype.** SMF 98033, an adult male from Filo del Tallo, on main road (via Puerto Kimba) adjacent to the park (Filo del Tallo), 8.450981°N, 78.00002°W, 128 m elevation, Darién, Panama, collected 23 June 2012 by Kirsten E. Nicholson, Sarah Burton, John G. Phillips, and David Laurencio. Field tag number KEN 0955.

**Diagnosis.** A small species (SVL in only known adult male 54.5 mm) of the genus *Norops* (sensu Nicholson *et al.* 2012) that differs from all Mexican and Central American anoles by having a combination of (1) smooth, bulging, subimbricate ventral scales; (2) a short tail, ratio tail length/SVL 1.54; (3) short hind legs, longest toe of adpressed hind leg reaching to ear opening, ratio shank length/SVL 0.24; (4) a lichenous body pattern; and (5) a very large yellowish orange dewlap in males. In external morphology, *N. triumphalis* is most similar to the species of the *N. pentaprion* group (see introduction). *Norops triumphalis* differs from the other species in the *N. pentaprion* group except *N. sulcifrons* by having a very large orange male dewlap (vs. a large red or pink dewlap) and an unpigmented throat lining. *Norops triumphalis* differs from *N. sulcifrons* by having the supracaudal scales not forming a serrated crest (vs. a distinct serrated caudal crest present in *N. sulcifrons*), 4 supracaudal scales per segment (vs. 3 supracaudal scales per segment in *N. sulcifrons*), greatly enlarged outer postmental scales, about four times the size of adjacent medial scales (vs. moderately enlarged outer postmental scales, about twice the size of adjacent medial scales, in *N. sulcifrons*), and no enlarged postcloacal scales in males (vs. a pair of moderately enlarged postcloacal scales present in male *N. sulcifrons*). *Norops triumphalis* differs from *N. ibague* and *N. ortonii* by having bulging, granular to subimbricate ventral scales at midbody (vs. flat and imbricate in *N. ibague* and *N. ortonii*). *Norops triumphalis* differs further from *N. ibague* by having 2 scales between interparietal and supraorbital semicircles (vs. interparietal and supraorbital semicircles broadly in contact in *N. ibague*).

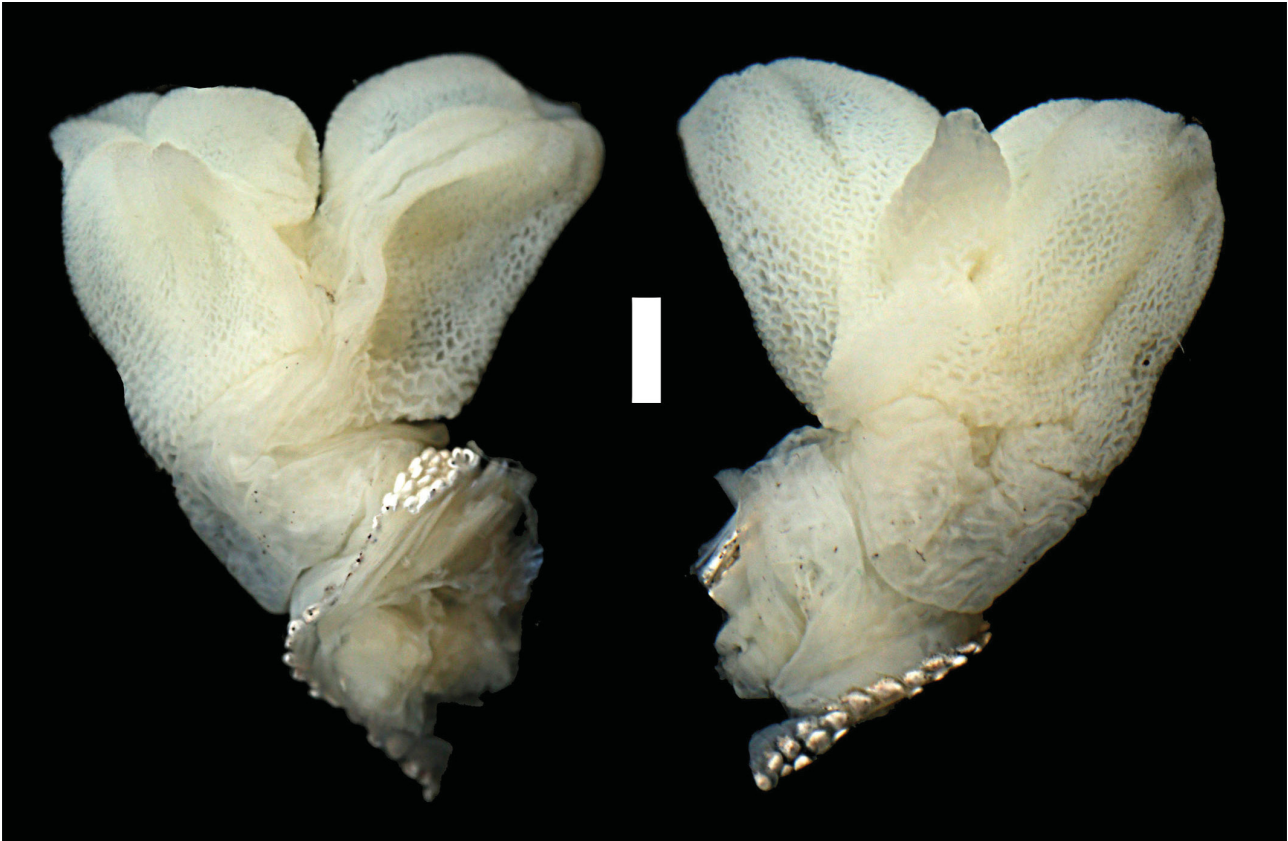


**FIGURE 1.** Holotype of *Norops triumphalis* (SMF 98033) in life. Photo: John G. Phillips.



**FIGURE 2.** Dewlap of *Norops triumphalis* (SMF 98033) in life. Photo: John G. Phillips.



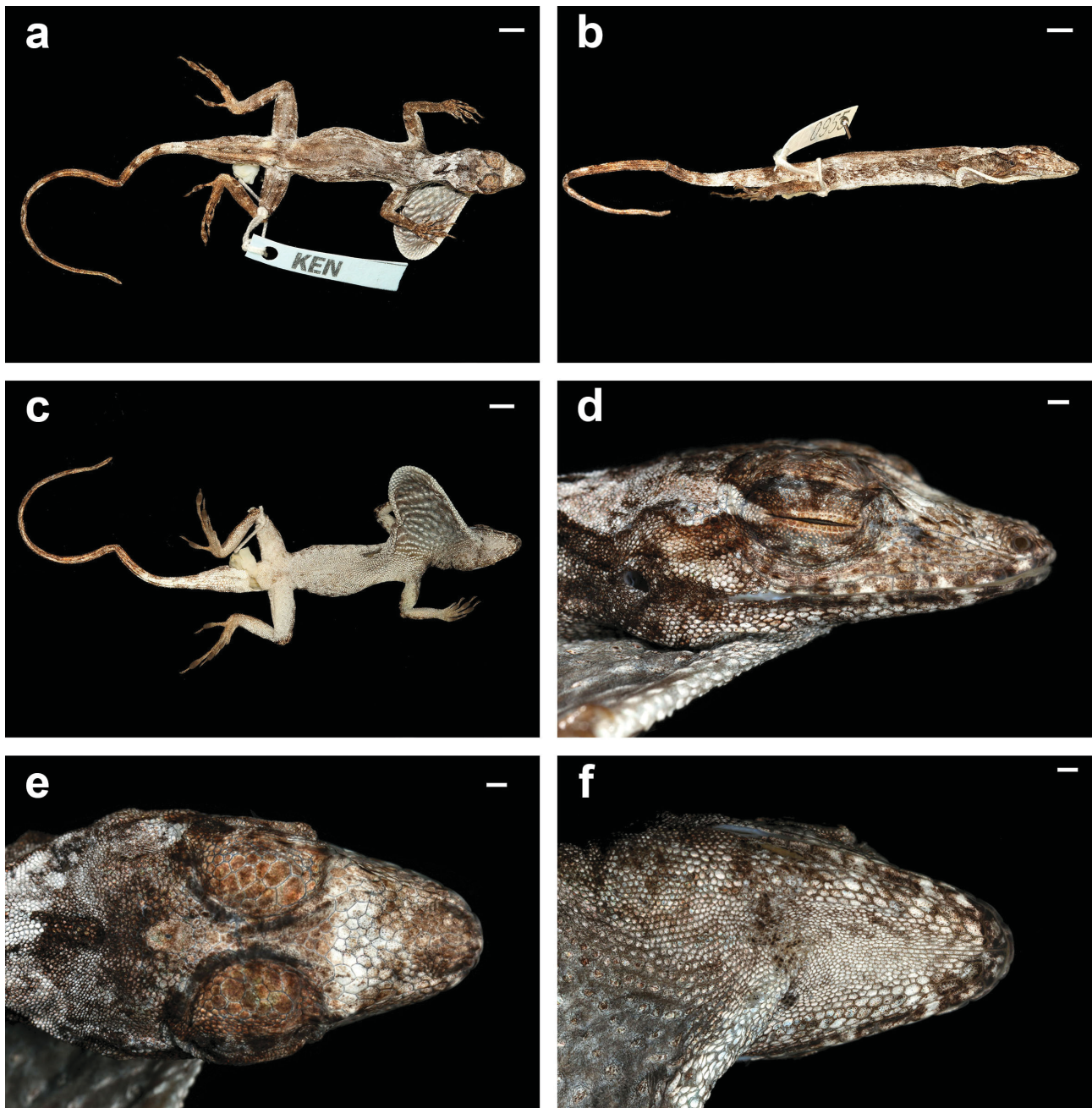


**FIGURE 3.** Hemipenis of *Norops triumphalis* (SMF 98033); sulcate view left, asulcate view right. Scale bar equals 1.0 mm.

**Description of the holotype.** Adult male, as indicated by everted hemipenes and presence of large dewlap; SVL 54.5 mm; tail length 84.0 mm, tail complete; tail slightly compressed in cross section, tail height 2.6 mm and width 2.0 mm; axilla to groin distance 22.6 mm; head length 14.3 mm, head length/SVL ratio 0.26; snout length 6.6 mm; head width 8.5 mm; longest toe of adpressed hind limb reaching to ear opening; shank length 13.2 mm, shank length/head length ratio 0.92; longest finger of extended forelimb reaching to nostril; longest finger of adpressed forelimb reaching to anterior insertion of hind limbs. Dorsal head scales in internasal region mostly keeled or rugose, other dorsal head scales smooth or rugose; 6 postrostrals; 6 scales between nasals; 1 prenasal scale on both sides, in contact with both rostral and first supralabial; circumnasal in contact with first supralabial; scales in deep prefrontal depression mostly smooth, some rugose; supraorbital semicircles well developed, broadly in contact medially (2 scales broadly in contact with each other); supraorbital disc composed of 6 moderately enlarged scales, arranged in 2–3 rows; circumorbital row complete, therefore, enlarged supraorbital scales completely separated from supraorbital semicircles; 2 elongated, strongly overlapping superciliaries, anterior one larger than posterior one, followed posteriorly by 2 elongate and then by about 6 roundish to squarish scales of moderate size; 2–4 rows of small smooth scales extending between enlarged supraorbitals and superciliaries; a shallow parietal depression present; interparietal scale well developed, 1.8 x 1.2 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 3 large (anterior one smallest) and 3 small anterior canthal scales; 11 scales present between second canthals; 10 scales present between posterior canthals; 33 mostly smooth to rugose loreal scales in a maximum of 6 (right)–7 (left) horizontal rows; 5 keeled subocular scales arranged in a single row; 6 (right)–7 (left) supralabials to level below center of eye; 3–4 suboculars broadly in contact with 3–4 supralabials; ear opening 0.6 x 1.1 mm (length x height); mental distinctly wider than long, completely divided medially, bordered posteriorly by 6 postmentals, outer ones much larger than median ones; 6 infralabials to level below center of eye; 2 greatly enlarged sublabials in contact with infralabials on both sides; smooth granular scales present on chin and throat; dewlap large (670 mm<sup>2</sup>), extending from level below anterior margin of eye to level of chest; dorsum of body with smooth, bulging to conical granular scales with rounded posterior margins; 2–4 medial rows scarcely enlarged; largest dorsal scales

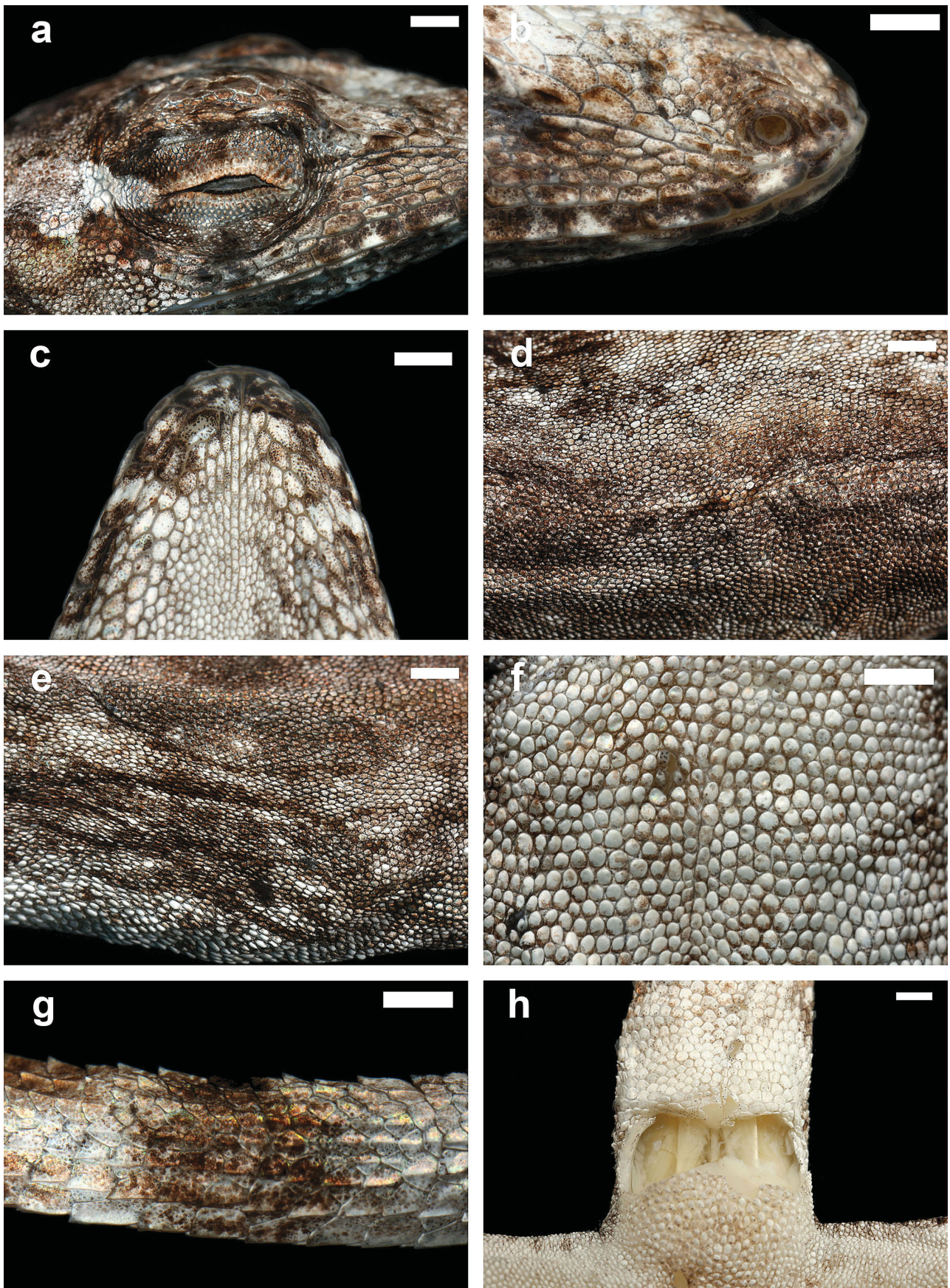


about 0.20 x 0.16 mm (length x width); about 67 medial dorsal scales in one head length; about 102 medial dorsal scales between levels of axilla and groin; lateral scales smooth, granular and slightly heterogeneous in size, average size 0.13 mm in diameter; ventrals at midbody smooth, bulging, granular to subimbricate with rounded posterior margins, about 0.30 x 0.20 mm (length x width); about 57 medial ventral scales in one head length; about 79 medial ventral scales between levels of axilla and groin; 179 scales around midbody; caudal scales keeled except ventrally at base of tail; middorsal caudal scales moderately enlarged, not forming a crest; lateral caudal scales without whorls of enlarged scales, although an indistinct division in segments is discernible; 4 supracaudal scales per segment; postcloacal scales not enlarged; no tube-like axillary pocket present although a shallow axillary depression is discernible; scales on dorsal surface of forelimb smooth to rugose, subimbricate to imbricate; digital pads dilated, dilated pad about 3–4 times width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 27 (right)–29 (left) lamellae under phalanges II–IV of Toe IV of hind limbs; 8 scales under distal phalanx of Toe IV of hind limbs.



**FIGURE 4.** Holotype of *Norops triumphalis* (SMF 98033). (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 5.0 mm in (a–c) and 1.0 mm in (d–f), respectively.





**FIGURE 5.** Holotype of *Norops triumphalis* (SMF 98033): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) lateral view of tail; (h) cloacal region. Scale bars equal 1.0 mm.



The completely everted hemipenis (Fig. 5) is a large bilobate organ; sulcus spermaticus bordered by well developed sulcal lips and bifurcating into two branches that continue to the tips of the lobes; a finger-like asulcate processus present; apex strongly calyculate, truncus and asulcate ridge with transverse folds.

The extended dewlap in life has about 7 somewhat irregular horizontal gorgetal-sternal rows with a declining number of scales per row from base to tip (12–15 scales per row on basal portion, 6 towards tip).

Coloration in life was recorded as follows: Dorsal ground color Light Neutral Gray (297) with irregular Smoky White (261) and Dusky Brown (285) markings and suffusion producing a lichenous appearance; dorsal surface of head Vandyke Brown (281) with a Smoky White (261) transverse band across snout just anterior to eyes; dorsal and lateral surfaces of tail Smoky White (261) with Brownish Olive (276) bands; dewlap Spectrum Yellow (79) with Chrome Orange (74) suffusions around Smoky White (261) to Dusky Brown (285) gorgetals; iris Orange-Rufous (56).

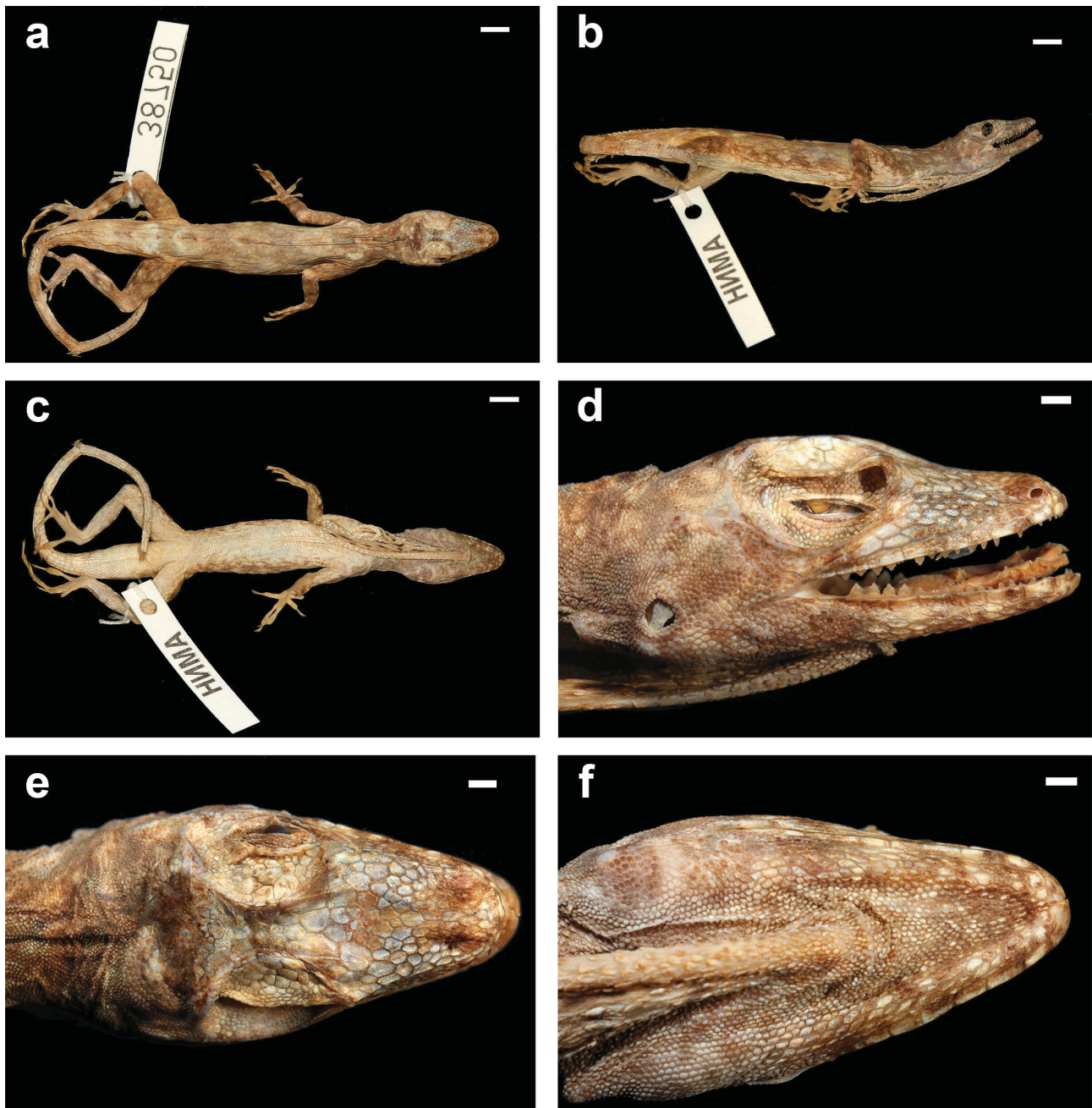
Coloration after about 16 months preservation in 70% ethanol was recorded as follows: Dorsal surfaces of head, body, limbs, and tail with a lichenous pattern of irregular Pale Neutral Gray (296), Glaucous (289), and Fuscous (283) markings and suffusions; ventral surface of head Light Neutral Gray (297) suffused with Brownish Olive (292); ventral surfaces of body and legs Smoke Gray (266); ventral surface of tail Grayish Horn Color (268) with Smoky White (261) bands on anterior portion; ventral surfaces of hands and feet Glaucous (272); dewlap Drab-Gray (256) with Medium Neutral Gray (298) and Smoky White (261) gorgetals.

**Etymology.** The name *triumphalis* (Latin for “of victory”) is an adjective referring to the moment of elation experienced by KEN and her field party at the moment of capture of the holotype of this species, given that the specimen was racing across the road in front of their moving vehicle.



**FIGURE 6.** Habitat at the type locality of *Norops triumphalis*. Photo: David Laurencio.



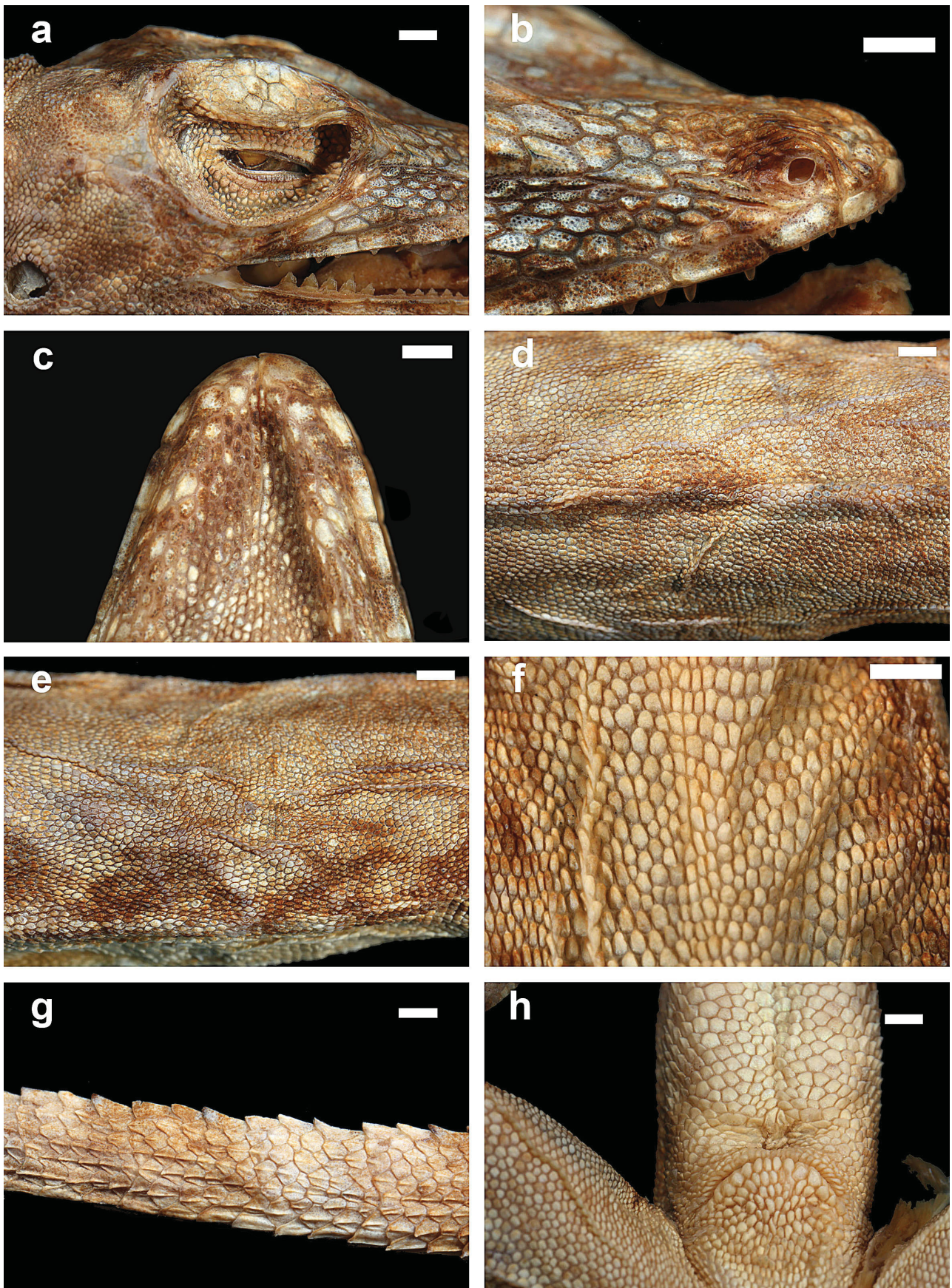


**FIGURE 7.** Holotype of *Norops sulcifrons* (AMNH 38750). (a) dorsal view; (b) lateral view; (c) ventral view; (d) lateral view of head; (e) dorsal view of head; (f) ventral view of head. Scale bars equal 5.0 mm in (a–c) and 1.0 mm in (d–f), respectively.

**Natural history notes.** The holotype was discovered in an open area while KEN and her field crew were traveling slowly along a road around the park and where there was a steep mountain that forms Filo del Tallo. This was in a pasture area with a fence row along the road (Fig. 6). This specimen had darted across the road that was bordered by thick grass on both sides but was actually captured on the small, paved road during the day, at 14.41 h. At the same location a *Norops vittigerus* was captured head down on a wooden fence post interspersed with living trees as part of the fence. The capture site was a few hundred meters away from a few small homes of farmers and the area was heavily agricultural with signs of recent visitation by cattle, although none were present at the time of capture.

**Notes on *Norops sulcifrons*.** In 1899, Cope described the new species *Anolis sulcifrons* based on a specimen (holotype now AMNH 38750) from “New Granada...in Colombia...most of them, it is believed, were found in the neighborhood of Bogota.” This nominal taxon was regarded as a synonym of *Norops* (or *Anolis*) *pentaprion* by most authors (e.g., Barbour 1934, Dunn 1944, Peters & Donoso-Barros 1970) until Myers (1971) resurrected it.





**FIGURE 8.** Holotype of *Norops sulcifrons* (AMNH 38750): (a) superciliary region; (b) nasal region; (c) chin region; (d) dorsal region (e) flank region; (f) midventer; (g) lateral view of tail; (h) cloacal region. Scale bars equal 1.0 mm.



The type locality of the holotype was restricted to “Barranquilla,” Colombia, by Smith & Taylor (1950:363), but Dunn & Stuart (1951) rejected this type locality restriction. Peters & Donoso-Barros (1970:62) stated that the holotype had come “perhaps from Bogotá, Colombia.” Because the holotype of *Norops sulcifrons* was never described in detail, we provide the following standard description of AMNH 38750 (Figs. 7 and 8).

**Description of the holotype of *Norops sulcifrons* (AMNH 38750).** Adult male, as indicated by presence of large dewlap and swollen base of tail indicative of the presence of hemipenes; SVL 63.0 mm; tail incomplete; tail slightly compressed in cross section, tail height 3.0 mm and width 2.2 mm; axilla to groin distance 25.7 mm; head length 15.8 mm, head length/SVL ratio 0.25; snout length 7.9 mm; head width 9.5 mm; shank length 14.5 mm, shank length/head length ratio 0.92. Dorsal head scales in internal region mostly keeled or rugose, other dorsal head scales smooth or rugose; 7 postrostrals; 7 scales between nasals; 1 prenasal scale on both sides, in contact with both rostral and first supralabial; circumnasal in contact with first supralabial; scales in deep prefrontal depression mostly smooth, some rugose; supraorbital semicircles well developed, separated by one scale row at narrowest point; supraorbital disc composed of 5 moderately enlarged scales, arranged in 2–3 rows; circumorbital row complete on left side, incomplete on right side, therefore one enlarged supraorbital scale in contact with supraorbital semicircle on right side; 2 elongated, strongly overlapping superciliaries, anterior one larger than posterior one, followed posteriorly by 1 elongate and then by about 5 roundish to squarish scales of moderate size; 3–4 rows of small smooth scales extending between enlarged supraorbitals and superciliaries; a moderate parietal depression present; interparietal scale well developed, 2.0 x 1.6 mm (length x width), surrounded by scales of moderate size; 2 scales present between interparietal and supraorbital semicircles; canthal ridge distinct, composed of 4 (right)–3 (left) large (anterior one smallest) and 3 small anterior canthal scales; 8 scales present between second canthals; 10 scales present between posterior canthals; 29 (right)–36 (left) mostly smooth to rugose loreal scales in a maximum of 6 horizontal rows on both sides; 5 keeled subocular scales arranged in a single row; 6 (right)–7 (left) supralabials to level below center of eye; 3–4 suboculars broadly in contact with 4–5 supralabials; ear opening 1.0 x 1.1 mm (length x height); mental distinctly wider than long, completely divided medially, bordered posteriorly by 6 postmentals, outer ones about twice the size of median ones; 7 (right)–8 (left) infralabials to level below center of eye; sublabials not differentiated; smooth granular scales present on chin and throat; dewlap large, extending from level below anterior margin of eye to level of chest; dorsum of body with smooth, bulging to conical granular scales with rounded posterior margins; 2–4 medial rows scarcely enlarged; largest dorsal scales about 0.22 x 0.16 mm (length x width); about 58 medial dorsal scales in one head length; about 88 medial dorsal scales between levels of axilla and groin; lateral scales smooth, granular and slightly heterogeneous in size, average size 0.20 x 0.12 mm (length x width); ventrals at midbody smooth, bulging, granular to subimbricate with rounded posterior margins, about 0.40 x 0.20 mm (length x width); about 46 medial ventral scales in one head length; about 66 medial ventral scales between levels of axilla and groin; 170 scales around midbody; caudal scales keeled except ventrally at base of tail; middorsal caudal scales greatly enlarged and forming a crest; lateral caudal scales without whorls of enlarged scales, although an indistinct division in segments is discernible, 3 supracaudal scales per segment; a pair of moderately enlarged postcloacal scales present; no tube-like axillary pocket present; scales on dorsal surface of forelimb rugose to weakly keeled, subimbricate to imbricate; digital pads dilated, dilated pad about 4 times width of non-dilated distal phalanx; distal phalanx narrower than and raised from dilated pad; 29 (right)–28 (left) lamellae under phalanges II–IV of Toe IV of hind limbs; 8 scales under distal phalanx of Toe IV of hind limbs.

## Discussion

This contribution increases to eleven the number species in the group of anoles related to *Norops pentaprion*. Despite the extensive geographic range of the group (Köhler 2008), none of these species are frequently encountered, and thus little is known about them. As mentioned above, they could be equated with Williams’ (1983) twig ecomorph, although typical for mainland species they are not identical to the Caribbean twig ecomorphs ecologically or morphologically (Pinto *et al.* 2008). The *N. pentaprion* group’s cryptic coloration and habits make them difficult to observe. Little is known regarding their evolutionary relationships as well, and while it is assumed that this group is monophyletic, that hypothesis has never been studied. A combination of ecological, behavioral, and molecular data would allow a thorough investigation of the evolution of this group and an excellent



opportunity to compare them to Caribbean twig ecomorphs. Such a comparison would be highly informative with respect to understanding the evolution of adaptive radiations and constraints within anoles.

## Acknowledgments

Collecting and exportation permits (Permiso científico number SEX/A-50-12) were issued by UNARGEN, Autoridad Nacional del Ambiente (ANAM), Panama City, Panamá, Panama. For the loan of and/or access to specimens, we thank L. Ford, C. J. Raxworthy and D. R. Frost, American Museum of Natural History (AMNH), New York; T. Daeschler and N. Gilmore, Academy of Natural Sciences (ANSP), Philadelphia; C. J. McCarthy, The Natural History Museum (BMNH), London; J. Vindum, California Academy of Sciences (CAS), San Francisco; S. P. Rogers, Carnegie Museum of Natural History (CM), Pittsburgh; C. Pozo and E. Escobedo Cabrera, Museo de Zoología-Ecosur (ECOCHH), Chetumal, Quintana Roo, Mexico; N. M. Ferrer, J. C. López Vidal and S. A. Murillo Jiménez, Instituto Politécnico Nacional, Escuela Nacional de Ciencias Biológicas (ENCB), Mexico City; A. Resetar, Field Museum of Natural History (FMNH), Chicago; V. H. Reynoso, Universidad Nacional Autónoma de México, Instituto de Biología (IBH), Mexico City; R. Luna, Colección Herpetológica del Instituto de Historia Natural (IHNHERP), Tuxtla Gutiérrez, Chiapas, Mexico; G. Lenglet, Institut Royal des Sciences Naturelles de Belgique (IRSNB), Bruxelles; W. E. Duellman and J. E. Simmons, University of Kansas, Natural History Museum (KU), Lawrence; J. Seigel, Natural History Museum of Los Angeles County (LACM), Los Angeles; D. Rossman, Museum of Natural Science, Louisiana State University (LSUMZ), Baton Rouge; J. Hanken and J. P. Rosado, Museum of Comparative Zoology, Harvard University (MCZ), Cambridge; S. Poe, Museum of Southwestern Biology, University of New Mexico (MSB), Albuquerque; N. Jiménez, Museo Zoológico de la Universidad de Ciencias y Artes del Estado de Chiapas (MZ-UNICACH), Tuxtla Gutiérrez; A. Nieto Montes De Oca, Museo de Zoología “Alfonso Herrera” (MZFC), Universidad Autónoma de México, México D.F.; F. Bolaños, G. Chaves and A. García R., Museo de Zoología Universidad de Costa Rica (UCR), San José; K. L. Krysko and F. W. King, Florida Museum of Natural History (UF), Gainesville; C. A. Phillips and J. Petzing, Illinois Natural History Survey, Center for Biodiversity (UIMNH), Champaign; R. A. Nussbaum and G. Schneider, University of Michigan Museum of Zoology (UMMZ), Ann Arbor; R. W. McDiarmid and W. R. Heyer, National Museum of Natural History (USNM), Washington, D.C.; J. Campbell and C. Franklin, The University of Texas at Arlington (UTA), Arlington; D.C.; M. Dix, M. Maldonado, and M. J. Illescas, Universidad del Valle de Guatemala (UVG), Guatemala City. For field assistance, KEN thanks S. Burton, J. G. Phillips, and D. Laurencio. J. G. Phillips, and D. Laurencio provided photographs used in this contribution. KEN received funding from NSF (DEB 0949359) and Central Michigan University.

## References

- Barbour, T. (1934) The anoles. II. The mainland species from Mexico southward. *Bulletin of the Museum of Comparative Zoology, Harvard University*, 77, 121–155.
- Boulenger, G.A. (1881) Description of a new species of *Anolis* from Yucatan. *Proceedings of the Zoological Society London*, 1881, 921–922.  
<http://dx.doi.org/10.1111/j.1096-3642.1881.tb01350.x>
- Boulenger, G.A. (1885) *Catalogue of the lizards in the British Museum (Natural History). Vol. II. 2<sup>nd</sup> Edition*. Trustees of the British Museum, London, i–vi, 497 pp.  
<http://dx.doi.org/10.5962/bhl.title.21097>
- Castañeda, M.d.R. & de Queiroz, K. (2013) Phylogeny of the *Dactyloa* clade of *Anolis* lizards: New insights from combining morphological and molecular data. *Bulletin of the Museum of Comparative Zoology*, 160, 345–398.  
<http://dx.doi.org/10.3099/0027-4100-160.7.345>
- Cope, E.D. (1862) Contributions to Neotropical saurology. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14, 176–188.
- Cope, E.D. (1868) An examination of the Reptilia and Batrachia obtained by the Orton Expedition to Equador and the Upper Amazon, with notes on other species. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 20, 96–140.
- Cope, E.D. (1899) Contributions to the herpetology of New Granada and Argentina with descriptions of new forms. On a collection of Batrachia and Reptilia from New Granada. *The Philadelphia Museums Science Bulletin*, 1, 1–19.  
<http://dx.doi.org/10.5962/bhl.title.54674>

- Dunn, E.R. (1944) Herpetology of the Bogota area. *Revista de la Academia Colombiana de Ciencias Exactas, Física y Naturales*, 6, 68–81.
- Dunn, E.R. & Stuart, L.C. (1951) Comments on some recent restrictions of type localities of certain South and Central American amphibians and reptiles. *Copeia*, 1951, 55–61.  
<http://dx.doi.org/10.2307/1438054>
- Frost, D.R. & Kluge, A.G. (1994) A consideration of epistemology in systematic biology, with special reference to species. *Cladistics*, 10, 259–294.  
<http://dx.doi.org/10.1111/j.1096-0031.1994.tb00178.x>
- Köhler, G. (1996) A new species of anole of the *Norops pentapryon* group from Isla de Utila, Honduras. *Senckenbergiana Biologica*, 75, 23–31.
- Köhler, G. (2008) *Reptiles of Central America*. 2<sup>nd</sup> Edition. Herpeton, Offenbach, 400 pp. [Germany]
- Köhler, G. (2010) A revision of the Central American species related to *Anolis pentapryon* with the resurrection of *A. beckeri* and the description of a new species (Squamata: Polychrotidae). *Zootaxa*, 2354, 1–18.
- Köhler, G. (2012) *Color Catalogue for Field Biologists*. Herpeton, Offenbach, 49 pp.
- Köhler, G. (2014) Characters of external morphology used in *Anolis* taxonomy—Definition of terms, advice on usage, and illustrated examples. *Zootaxa*, 3774 (3), 201–257.  
<http://dx.doi.org/10.11646/zootaxa.3774.3.1>
- Myers, C.W. (1971) Central American lizards related to *Anolis pentapryon*: Two new species from the Cordillera de Talamanca. *American Museum Novitates*, 2471, 1–40.
- Nicholson, K.E., Crother, B.I., Guyer, C. & Savage, J.M. (2012) It is time for a new classification of anoles (Squamata: Dactyloidae). *Zootaxa*, 3477, 1–108.
- Nicholson, K.E., Crother, B.I., Guyer, C. & Savage, J.M. (2014) Anole classification: A response to Poe. *Zootaxa*, 3814 (1), 109–120.  
<http://dx.doi.org/10.11646/zootaxa.3814.1.6>
- Peters, J.A. & Donoso-Barros, R. (1970) Catalogue of the Neotropical Squamata. Part II. Lizards and Amphisbaenians. *United States National Museum Bulletin*, 297, 1–293.  
<http://dx.doi.org/10.5479/si.03629236.297.1>
- Pinto, G., Mahler, D.L., Harmon, L.J. & Losos, J.B. (2008) Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards. *Proceedings of the Royal Society of London B: Biological Sciences*, 275 (1652), 2749–2757.  
<http://dx.doi.org/10.1098/rspb.2008.0686>
- Poe, S. (2013) 1986 Redux: New genera of anoles (Squamata: Dactyloidae) are unwarranted. *Zootaxa*, 3626 (2), 295–299.  
<http://dx.doi.org/10.11646/zootaxa.3626.2.7>
- Sabaj Pérez, M.H. (Ed.) (2014) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 5.0 (30 October 2014). American Society of Ichthyologists and Herpetologists, Washington, DC. Available from: <http://www.asih.org/resources/standard-symbolic-codes-institutional-resource-collections-herpetology-ichthyology> (accessed 30 October 2014)
- Simpson, G.G. (1961) *Principles of Animal Taxonomy*. Columbia University Press, New York, New York, 262 pp.
- Smith, H.M. (1968) A new pentapryonid anole (Reptilia: Sauria) from Pacific slopes of Mexico. *Transactions of the Kansas Academy of Science*, 71 (2), 195–200.  
<http://dx.doi.org/10.2307/3627371>
- Smith, H.M. & Taylor, E.H. (1950b) Type localities of Mexican reptiles and amphibians. *University of Kansas Science Bulletin*, 33, 313–380.
- Wiley, E.O. (1978) The evolutionary species concept reconsidered. *Systematic Zoology*, 27, 17–26.  
<http://dx.doi.org/10.2307/2412809>
- Williams, E.E. (1975) South American *Anolis*: *Anolis ibague*, new species of the *pentapryon* group from Colombia. *Breviora*, 433, 1–10.
- Williams, E.E. (1983) Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In: Huey, R.B., Pianka, E.R. & Shoener, T.W. (Eds.), *Lizard ecology: studies of a model organism*. Harvard University Press, Cambridge, pp. 326–370.

## APPENDIX 1. Comparative material examined.

*Anolis beckeri*—**Belize**: Cayo: Five Sister Lodge; 16 mi S on Caracol Rd. then W 2 mi: POE field number 1217, 1183–84; San Ignacio, 12 mi SW of, Xunantunich ruins: USNM 220398. **Guatemala**: Chiquimula: Ceiba: UMMZ 79081; Izabal: Morales, Sierra de Caral, Camino Quebradas-La Firmeza: UTA R39784; Fronteras: Puente de Río Dulce: UVG 452; El Petén: Parque Nacional Tikal: UF 13773, 24616, UMMZ 117822; Flores, Carretera de Yaxha a Nakum: UVG 1355. **Honduras**: Atlántida: Guaymas District [=an old United Fruit Company Plantation located 40 km WSW of Tela at 10 m elev.]: UMMZ 58392–95; Lancetilla, MCZ 38835; Colón: mountains just S of Trujillo: CM 64619; Salamá: USNM 242056; Cerro Calentura, LSUMZ 33678; Gracias a Dios: Palacios, BMNH 1985.1121; Olancho: Montana del Ecuador,

1400 m: USNM 344805. **Mexico:** Campeche: 24 Km N X-Pujil, Entrada a “El Papagayo”: ECOCHH 0559; Zona Arqueológica de Calakmul: ECOCHH 0835; 64 Km N X-Pujil, Km 2.5 on road to Rancho San Isidro: ECOCHH 0964; Chiapas: Cascadas de Agua Azul: MZFC 489; Zona Arqueológica de Yaxchilán, Ocosingo: MZFC 12207; Rancho Alejandria, 6 km SE Estación Juárez, Municipio Juárez, 60 m: IHNHERP 559, 652; Reforma Agracia, Zona Marques de Camillas, Ocosingo: MZ-UNICACH 241; Palenque: MCZ 93676–77, USNM 136491; San Juanito: UIMNH 37067–90, USNM 136492–516; Lake near Acacoyagua: USNM 136490; Quintana Roo: Chetumal: ECOCHH 1437; 1 Km N de Nuevo Becal, Aguada: ECOCHH 1417; Ejido Tres Garantías: ECOCHH 2311-12; Tres Garantías Aguadas Burgos: ECOCHH 2273; Veracruz: Las Choapas, Colonia Bateria Los Soldados: MZFC 16574; Yucatán: no specific locality: IRSNB 2010 (1–2).

*Anolis charlesmyersi*—**Costa Rica**: Alajuela: Balsa: UCR 12422; Hwy 3 between Atenas and Coyolar: SMF 89353; Guanacaste: Finca La Pacifica, 4 km NW Cañas: LACM 148372, 148377; Finca La Pacifica, Río Corobici (margin): LACM 148393; Río Sandillal at Interamerican Highway: LACM 148386, 148392, 148394; Sta. Rosa, Mirador Valle Naranjo: UCR 14642; Vieja Tronadora: UCR 2903; Pueblo Viejo: UCR 14931; Casona at Santa Rosa, 300 m: UCR 18022; Puntarenas: 3.5 mi SW Rincón: UF 135769; 4.5 km W Rincón de Osa: KU 102418; Aguabuena: UCR 4950, 11755; ca. 1.5 km SW of Rincón de Osa, Osa Tropical Science Center,: USNM 219557–60; Dos Bocas, Fila San Andrés: UCR 14565; EB Marengo: UCR 15117; Golfito: UCR 12245, 14227, 18315; Guapil, near Dominical, 100 m: POE field number 2266, 2616–17; Hacienda Barú: UCR 2438, 14316–18, 14774; La Gamba, Esquinas Lodge: UCR 12698; Palmar: KU 34254–55; Península de Osa, Golfo Dulce, Puerto Jiménez, jardín at Jiménez Yacht Club: SMF 81506; Pl. Palma: UCR 13599; Punta Mala: UCR 11012; Rincón de Osa: UCR 2542, 5279; Tres Piedras: UCR 15916; Hatillo: Sabina's: POE field number 2563; 5 km NW of Río Salena Nuevo on Hwy 2: LACM 148379; San Jose: Near Piedras Negras, Río Virilla Crossing, 490 m: POE field number 2224; Alto Palma: UCR 11121; Brasil: UCR 7467; C. Chirripó, Llano Bonito: UCR 11942. **Panama**: Chiriquí: Los Algarrobos, trail to Río Majagua: MHCH 2137, SMF 89508, 89688; Universidad Autonoma de Chiriquí, David: SMF 85056–57; Chiriquí or Veraguas: E of David (along PanAm; 20–100 km E of David): POE field number 1449–51.

*Anolis cristifer*—**Guatemala**: Quetzaltenango: El Palmar, Palajunoj, Finca El Patrocinio: SMF 82593; San Marcos: Hacienda California: MCZ 29771; Suchitepequez: Mazatenango: CAS 68214–15; Volcán Zunil: CAS 68216.

*Anolis fungosus*—**Panama**: Bocas del Toro: upper watershed of Río Changuena, north slopes of Cerro Pando, 1450 m: KU 113451; Chiriquí: Quebrada Arena, Reserva Forestal de Fortuna, 1074 m: SMF 86385.

*Anolis ibague*—**Colombia**: Tolima: Ibagué: NMW 18942:38.

*Anolis ortonii*—**Brasil**: Amazonas: lower Río Madeira: SMF 10972; Pará: Marajo: SMF 24842; Bahia: Caldeiras, Marjo: SMF 30391–405. **Ecuador**: Napo: Río Napo or upper Río Marañón, ANSP 11404; Pastaza: Arútam, SMF 86113–15.

*Anolis pentapryon*—**Costa Rica**: Cartago: 5 km SE Turrialba: UF 15946; 8 km W, 13 km N Turrialba: KU 67070; Santa Rosa de Turrialba: LACM 148397; Turrialba, CATIE, R. Reventazón: UCR 4999; Turrialba, IICA: LACM 148376, 148378; Heredia: 10 km S Puerto Viejo: LSUMZ 53173; 3 km SE Puerto Viejo: UF 31055, 31078–79, 31091, 31110–12, 31160–62; Río Frio, Standard Fruit Company: UF 30804, 30810, 30907, 30943–47, 31044–46, 31304, 31552, 31592, 31665, 32353; Sarapiquí: AMNH 16354; Limón: Pandora: MCZ 78389; Alto de Guayacán: UCR 14574; Colombiana: USNM 67349; San Miguel: UCR 12870. **Nicaragua**: Atlántico Sur: Río Siquia, 7 miles above Rama: UMMZ 79825; Granada: Volcán Mombacho: Photo provided by Eric van den Bergh; Río San Juan: Bartola: SMF 80961, 82100; Machuca: ANSP 7911; Río El Chanco, 5–6 km above junction with Río San Juan: SMF 83163; Rivas: Ometepe: Photo provided by S. Robledo. **Panama**: Bocas del Toro: 13.8 km S of turnoff to Almirante (14.5 km N of province boundary), Fortuna road, 235 m: POE field number 1855; Cerro Brujo, western portion of Laguna de Chiriquí: SMF 85058; hill behind Chiriquí Grande: AMNH 123262; Bocas del Toro: Isla Colon, N of mouth of Big Creek: USNM 347921; Isla Cristobal, Bocatorito camp: USNM 348211–12; Isla Popa, 1 km SE of Deer Island channel: USNM 298136; Laguna de Tierra Oscura, 3.7 km S of Tiger Key: USNM 348481; vicinity of Almirante: ANSP 34059; Coclé: between El Copé town and park entrance (creek crossing), 500 m: POE field number 1442–43; N of El Copé town, 500 m: POE field number 1537; Colón: Buena Vista: UF 102012–13; Canal Zone, Margarita: CM 22978; Viento Frio: USNM 48539; Comarca Ngöbe-Buglé: 13.8 km S of turnoff to Almirante (14.5 km N of province boundary), Fortuna road, 235 m: POE field number 1855; N of Fortuna, Caribbean slope: POE field number 1522; Los Santos: Los Santos: USNM 148221; Panamá: 8 km NNW Chepo, Madrona: UF 102000; Arraijan: USNM 163503; Balboa: AMNH 42926; Barro Colorado Island: AMNH 75987; ANSP 24540–42, KU 75960; Chilibre: UF 102001–02, 102004–05; Comunidad Embera, along Río Maje near Lake Bayamo, 305 m: POE field number 1655; El Aguacate: UF 102003, 102006–11, 102014; int. of Pan American Hwy and 'Nusagandi' road, 1km W of El Llano: POE field number 1556; near Aguacate, Cerro Trinidad: AMNH 103231; near Fort Clayton Reservation: UIMNH 42177–78, 42185; USNM 15131, 53888; Panama Viejo: KU 75959; Río Masambí: Photo Cesar Jaramillo; San José Island: USNM 120572–83; Veraguas: Bahía Honda: AMNH 62773.

*Anolis salvini*—**Panama**: Chiriquí: 4 km W Cerro Punta, 1829 m, AMNH 69621; Bambito, 6 mi S Cerro Punta, USNM 203831; above Boquete, ZFMK 27609–11; Palo Santo, 4 mi NW El Volcán, 4600 ft, ANSP 26287; Cerro Jurutungo, 8°54'30.5"N, 82°43'22.4"W, 1860 m, SMF 85451–52; Cerro La Pelota, 8°49'51"N, 82°36'50"W, 1580–1640 m, SMF 85453–57.

*Anolis sulcifrons*—“New Granada”: AMNH 38750.

*Anolis utilensis*—**Honduras**: Islas de la Bahía: Isla de Utila, 2 km NNE of Utila, SMF 77051–55, 77983, 79364–65, 79866.